

Patch Dynamics Inform Management Decisions in a Threatened Frog Species

Michael J. Lannoo¹, Rochelle M. Stiles¹, Michael A. Sisson², Jonathan W. Swan³, Vanessa C. K. Terrell⁴, and Kelly E. Robinson¹

Using a variety of techniques, we tracked dispersing juvenile and migrating adult Crawfish Frogs (*Lithobates areolatus*) to determine how these movements produce the relatively high degree of interconnectivity we previously found among breeding wetlands at Hillenbrand Fish and Wildlife Area-West (HFWA-W) in southwestern Indiana. We found that newly metamorphosed juveniles disperse in all directions, with average daily movements between 27 m (2015) and 35 m (2011) and maximum daily movements of 114 m (2011) and 297 m (2015). When placed in artificial burrows, juveniles tended to abandon them in order to continue dispersing. Of the 196 juveniles produced at Nate's Pond and subsequently captured as breeding adults, 141 (71.9%) returned to Nate's; the remainder dispersed to five other breeding wetlands, including one that was 1.35 km away. Adults were also vagile. At Nate's, only 137 (50.6%) of the 271 adults that bred there from 2012–2016 were produced there. Further, of the 255 Crawfish Frog adults breeding at least twice, 57 (22.4%) were captured at different wetlands. As a component of a comprehensive management plan that considers juvenile Crawfish Frogs, we suggest minimizing summertime aboveground disturbance through the use of mowers, all-terrain vehicles, trucks, and heavy equipment. Plowed areas such as food plots should be narrow and placed in a radial pattern in relation to breeding wetlands to preclude juveniles crossing tangentially oriented areas of bare ground, which expose them to predators.

CRAWFISH Frogs (*Lithobates areolatus*) are members of the subgenus *Nenirana* (Hillis and Wilcox, 2005), which may be the most endangered amphibian taxa in North America. Of the four species comprising this clade, three have serious conservation concerns. Dusky Gopher Frogs (*L. sevosus*) have been federally listed, Gopher Frogs (*L. capito*) have been petitioned for federal listing, and Crawfish Frogs have been discussed for federal listing (LaClaire, 2001; Williams et al., 2013; Richter et al., 2014). A recent assessment of the conservation status of Crawfish Frogs, compiled from local experts across their range, indicates they have been extirpated from 84 of the 243 counties (35%) they historically inhabited (Crawfish Frog Symposium, Kansas Herpetological Society Annual Meeting, November 2015, see <http://lannoolab.com/> for map). Populations east of the Mississippi River have been most heavily impacted.

We have been working out the life history/natural history features of Crawfish Frogs towards generating management recommendations to preempt federal listing. Pond-breeding amphibians have historically been characterized as having a limited capacity for dispersal, strong breeding site philopatry, and spatially segregated wetland-breeding sites. As Smith and Green (2005) observe, however, a closer look at the data suggests otherwise; there is evidence of extensive dispersal capabilities among amphibians, suggesting that breeding sites are more interconnected than previously assumed. Juveniles in particular have demonstrated a substantial capacity for dispersal (Gill, 1978; Breden, 1987; Berven and Grudzien, 1990; Funk et al., 2005; Gibbs and Reed, 2007).

We previously examined the genetics of Crawfish Frogs in the northern portion of their range and found: 1) observed heterozygosity values ranging between 0.54 and 0.67; 2) no genetic differentiation among breeding ponds <250 m apart; and 3) slight genetic divergence among breeding ponds ~750 m apart (Nunziata et al., 2013), suggesting Crawfish Frogs are not spatially segregating themselves, but that individuals are

moving among breeding wetlands. Here, we use mark-recapture techniques on both juveniles and adults, as well as radiotelemetry studies on juveniles, to explore the connectivity among Crawfish Frog breeding aggregations. Such knowledge will be critical in developing management plans for this species—a process that is just beginning.

MATERIALS AND METHODS

Study site.—Our study site was located on the western region of Hillenbrand Fish and Wildlife Area (HFWA-W) in Greene County, Indiana (Fig. 1). HFWA-W comprises 729 hectares that was historically eastern deciduous forest punctuated by pocket prairies (Transeau, 1935; Jones and Cushman, 2004; Whitaker et al., 2012). These native habitats were converted to agricultural fields beginning in the mid- to late-nineteenth century and extending into the twentieth century, prior to being surface mined for coal from 1976–1982 (Lannoo et al., 2009). Following mining, this area was re-contoured and seeded to herbaceous vegetation. In 1988, the property was purchased by the Indiana Department of Natural Resources (IDNR) for use as a state fish and wildlife area and was gradually re-seeded to native tallgrass prairie species, such as Big Bluestem (*Andropogon gerardii*), Little Bluestem (*Schizachyrium scoparium*), Indian Grass (*Sorghastrum nutans*), Partridge Pea (*Chamaecrista fasciculata*), and Black-eyed Susan (*Rudbeckia hirta*). HFWA-W is managed by the IDNR Division of Fish and Wildlife (Lannoo et al., 2009).

As a result of surface mining, post-mining habitat restoration, and erosion control, HFWA-W now contains a number of basins ranging in hydroperiod from ephemeral wetlands, through semi-permanent wetlands, to large final-cut lakes (Fig. 1; Kinney, 2011). (Explanation: The first step in surface mine reclamation is filling the pit, which is done using overburden. Because coal is being extracted, the amount of overburden available is always less than the volume of the pit. Therefore, the last portion of the mine

¹ Indiana University School of Medicine—TH, Terre Haute, Indiana 47809; Email: (MJL) mlannoo@iupui.edu; (RMS) rochelle.m.stiles@gmail.com; and (KER) kellyrobinson4788@gmail.com. Send reprint requests to MJL.

² North Carolina Wildlife Resources Commission, Wildlife Diversity Program, Raleigh, North Carolina 27699; Email: sissonh@aol.com.

³ Department of Biology, Indiana State University, Terre Haute, Indiana 47809; Email: Jonathan.W.Swan@gmail.com.

⁴ Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia 30602; Email: vkinney@uga.edu.

Submitted: 26 August 2016. Accepted: 5 December 2016. Associate Editor: J. W. Snodgrass.

© 2017 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CH-16-499 Published online: 10 March 2017

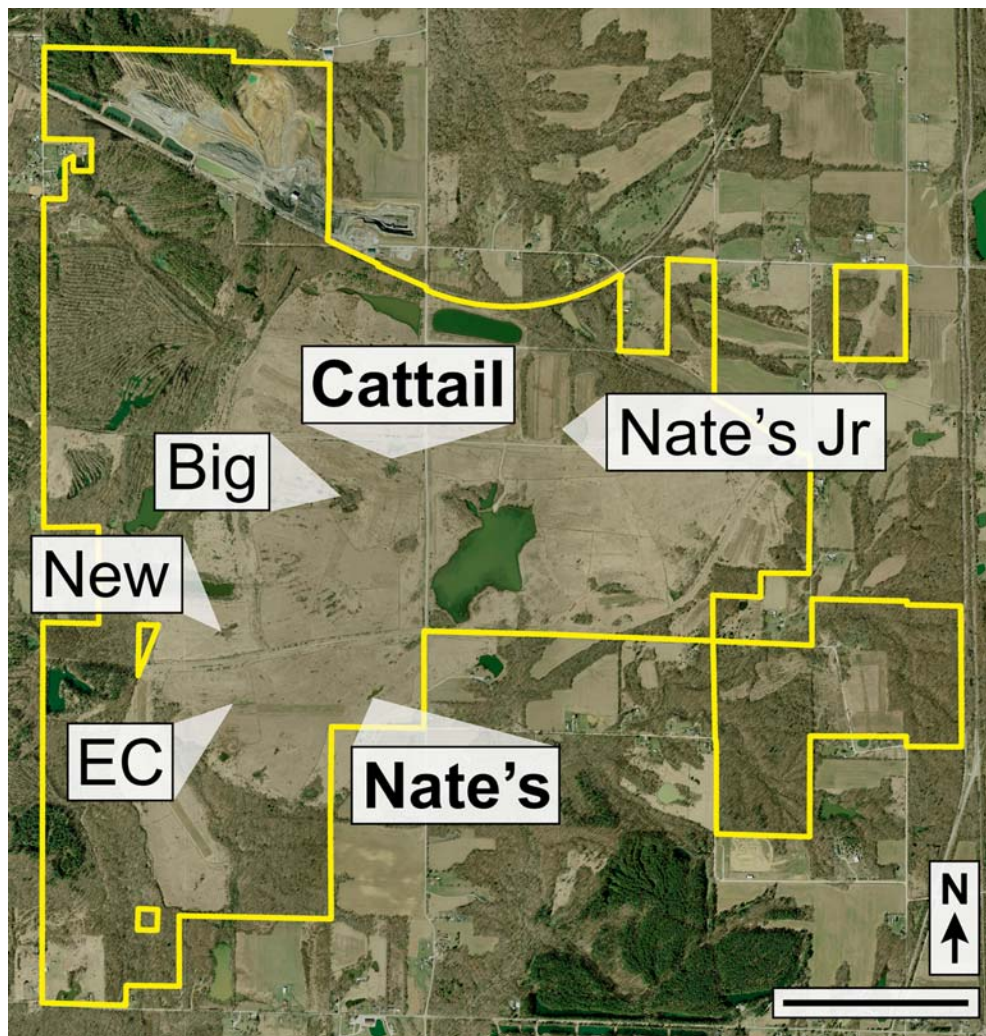


Fig. 1. Crawfish Frog breeding wetlands ($n = 6$) at Hillenbrand Fish and Wildlife Area-West (HFWA-W; Greene County, Indiana). We encircled Nate's and Cattail ponds (bolded text) with drift fence/pitfall trap arrays in 2009–2016 and sampled at the remaining wetlands (Big, Erosion Control [EC], New, and Nate's Jr.) using funnel traps. We monitored Crawfish Frog breeding (late February through early May) and metamorphosis (mid-June through early August) at Nate's and Cattail, and only breeding at the remaining wetlands. The yellow outline indicates the boundary of HFWA-W. Scale bar = 1 km.

excavated cannot be filled, leaving a deep gap, which fills naturally with water and is euphemistically termed a final-cut lake.) This work is part of a larger study conducted from 2009–2016 (Williams et al., 2013).

Dispersal from breeding wetlands.—Of the six wetlands used by Crawfish Frogs, we encircled two—Nate's and Cattail ponds—with drift fence/pitfall trap arrays (fully described by Kinney, 2011; Fig. 1), as follows. In 2009, we placed around these wetlands 1.2 m high, woven polypropylene composite fence, buried roughly 10–15 cm below ground, about 5 m from the wetland edge. We later installed hardware cloth in sections at drainage areas to prevent the washing out of drift fences due to flooding (Heemeyer et al., 2010). In 2010, we replaced the fence with more durable monofilament silt reinforced by wooden 5×60 cm laths screwed to the support stakes. Pitfall traps were 15 L white square buckets (23×23 cm opening, 33 cm depth) placed every 10 m in pairs along the inside and outside of the fencing (Heemeyer et al., 2010). We fitted each bucket with a half lid (open side closest to the fence) to provide shade for trapped animals and to deter predators (e.g., Raccoons [*Procyon lotor*], Skunks [*Mephitis mephitis*], Opossums [*Didelphis virginiana*], and feral Cats [*Felis catus*]). We added a sponge to each trap to prevent desiccation of animals during warm weather and to provide a floating substrate when buckets flooded, and we inserted a wooden stake ($2.5 \times 2.5 \times 40$ cm) into each trap to facilitate small mammal escape (Dodd and Scott, 1994).

We sampled the remaining four wetlands—Big, Erosion Control, New, and Nate's Jr.—using partially submerged funnel traps (Fig. 1). Traps were 61 cm by 30 cm and covered by black cotton mesh (15×10 mm mesh size; manufactured by American Maple, Inc., Gardena, CA; Klemish et al., 2013). We began sampling each trapped wetland after Crawfish Frog breeding choruses were heard (and continued sampling in subsequent years), as follows: Big in 2009, Erosion Control and New in 2011, and Nate's Jr. in 2013.

Our wetland sampling techniques allowed us to census breeding adults at Nate's and Cattail ponds (late February through early May; Kinney, 2011) and sample breeding adults at the remaining wetlands. We calculated an adult trespass rate of $<1.0\%$ at drift fences. Trespass rate is based on the number of individuals that crossed the fences without being detected. We determined this by counting animals that were either captured exiting but not entering, or captured entering but not exiting. Drift fence arrays also allowed us to census newly metamorphosed juveniles at Nate's and Cattail from mid-June through early August (2009–2015). Our data indicated that Cattail Pond is a sink. Despite an estimated 1.4 million eggs being deposited over the eight years of our study, fewer than 100 juvenile Crawfish Frogs were produced (survivorship $\sim 0.007\%$). Further, we have never observed a breeding adult from a Cattail Pond cohort. Given this, our analysis here is limited to Nate's Pond juveniles.

At Nate's Pond, newly metamorphosed juveniles were given toe clips coded to Nate's Pond (left hind foot toe clip)

and year (right front foot toe clip). These clips allowed us to identify natal cohort when these animals were captured two or three years later as breeding adults. With these data, we estimated juvenile survivorship to first breeding (see below). We gave each captured breeding adult a Passive Integrated Transponder (PIT) tag with either a unique 10 or 15 digit alphanumeric/numeric code (this study began with Bio-mark® supplying ten-digit alphanumeric PIT tags and ended with 15-digit numeric tags). PIT tags enabled us to determine adult survivorship as well as an animal's breeding history.

Given these marking techniques, we had two ways of assessing juvenile dispersal: animals dispersing from Nate's Pond, and animals dispersing to Nate's Pond. To determine dispersal from Nate's Pond, we recorded breeding adults in all wetlands marked with Nate's Pond toe clips. To determine dispersal into Nate's Pond, we recorded animals without toe clips. Because Crawfish Frogs require two or three years following metamorphosis to breed and we began our study in 2009, we started defining Nate's Pond adults without toe clips as originating from other ponds in 2012. Therefore, when comparing adults that originated from Nate's Pond with adults from other wetlands, we only analyzed captures from 2012–2015.

Juvenile telemetry.—To examine the dispersal of newly metamorphosed juvenile Crawfish Frogs from their natal wetlands, one of us (MAS) attached belted radio-transmitters (0.48 g, BD-2N; Holohil Systems Ltd., Carp, Ontario, Canada) to 25 individuals in 2011 (three additional animals were fitted with transmitters that generated no data). We constructed belts using 0.5 mm Stretch Magic® elastic cord, threaded through small (11/0) and large (6/0) glass beads (Muths, 2003). Sex and size has been shown to affect amphibian movements (Beck and Congdon, 2000; Bartelt et al., 2004; Grayson and Wilbur, 2009; for exceptions see Smith and Green, 2006); however, we could not sex juveniles (because juveniles do not display the paired vocal sacs or enlarged forearms of mature males) and had to choose among the largest juveniles in order for the combined weight of the radio-transmitter and belt to not exceed 10% of the frog's body mass (Richards et al., 1994), which reduces the risk of injury or death to individuals of this state endangered species. Adults tend to exhibit a 1:1 sex ratio (Kinney, 2011), and we assume this holds for juveniles also. We acknowledge that these practical concerns may create biases in our data.

We released telemetered juveniles at a point immediately outside the fence surrounding Nate's Pond, their natal wetland. We tracked frogs using a 3-element Yagi® unidirectional antenna and an R-1000 receiver (Communication Specialists, Orange, CA) and recorded locations (Global Position System coordinates) using a Garmin® GPSmap 76CSx (Olathe, KS) from 28 June–14 August. We attempted to relocate juveniles every morning during daylight. We measured distances between positions using ArcMap 10.1® (ESRI, 2011) and used these values to measure mean daily distance traveled, maximum daily distance, farthest straight-line distance from the release point, and total distance moved during the study.

Artificial burrows.—In 2015, one of us (JWS) constructed artificial burrows based on dimensions of previously observed burrows occupied by juvenile Crawfish Frogs (50 mm in diameter, dug at a 50° angle, 1.2 m deep; Heemeyer et al., 2012; Swan, 2016). We augured 78 burrows randomly placed

within a 9.4 ha area using a Badger Power Earth Auger (Model 81; Feldmann Engineering and Manufacturing Co., Sheboygan Falls, WI). To prevent habitation by other animals prior to Crawfish Frog release, we covered each burrow with a 3.8 L sand-filled bag.

We obtained juvenile Crawfish Frogs head-started at the Detroit Zoological Society (DZS) and originally collected as eggs from the study site (Stiles et al., 2016). At the time of release, we recorded each frog's age (days since metamorphosis), snout-to-vent length (SVL, mm), and mass (g), and marked each frog with a cohort toe clip (coded to the group, "captive-reared," and year). We released frogs at burrow entrances and monitored the fate of these animals using wildlife cameras (Bushnell Trophy Cam® Model 119436; Bushnell Outdoor Products, Overland Park, KS) programmed to take photographs at one-minute intervals, around-the-clock (Hoffman et al., 2010; Stiles et al., unpubl.). We released juveniles on 26 days from 24 June–1 August in batches of 1–12 frogs per release (n total = 149 juveniles).

We supplemented our wildlife camera data with radiotelemetry in 2015. Techniques and equipment were identical to our 2011 telemetry study, described above, with one exception: to prevent frogs from shedding transmitters and skin abrasion, belts were made from inelastic surgical thread (Vicryl™ [polyglactin 910] 5-0 RB1, #36; Ethicon, Somerville, NJ; technique modified from Muths, 2003). In 2015 only one juvenile (out of 12 [6%]) shed its belt compared to four juveniles (out of 28 [14%]) in 2011; in 2015 we removed a belt from one frog (out of 12 [6%]) with an injury from skin abrasion, compared to six juveniles (out of 28 [21%]) in 2011. We tracked 12 juveniles from 28 June–11 August 2015 and relocated frogs every morning during daylight.

Statistics.—We assessed juvenile and adult dispersal directionality from Nate's Pond using Welch's t-tests in Program R (R Core Team, 2016). For each year, we calculated the proportion of individuals exiting from each pitfall trap and averaged them across years. We separated traps along the long-axis of the wetland into northwest and southeast categories with equal sample sizes and compared the two categories for the following groups: juveniles (2009–2011, 2014), all adults (2009–2011, 2013–2016), adults from Nate's cohorts (2013–2016), and adults originating from other wetlands (2013–2016). We excluded years with small sample sizes (2012 for adults [$n = 14$] and 2013 for juveniles [$n = 8$]) and no juvenile recruitment (2012 and 2015) from the analyses and log transformed non-normal data.

To compare juvenile and adult dispersal from each trap, we calculated the ratio of the proportion of adults exiting over the proportion of juveniles exiting. We then compared directionality using a Welch's t-test and the methods described above. We excluded adults that originated from ponds other than Nate's.

To compare dispersal of the adult cohorts (Nate's Pond versus other wetlands), we used a paired t-test in Program R (R Core Team, 2016). The proportion of adults exiting from each trap each year was averaged across years (2013–2016) and compared between adults originating from Nate's and other wetlands. We excluded 2012 captures due to a small sample size ($n = 14$).

RESULTS

Juvenile dispersal: pitfall traps.—As assessed by pitfall trap locations, newly metamorphosed juveniles dispersed from

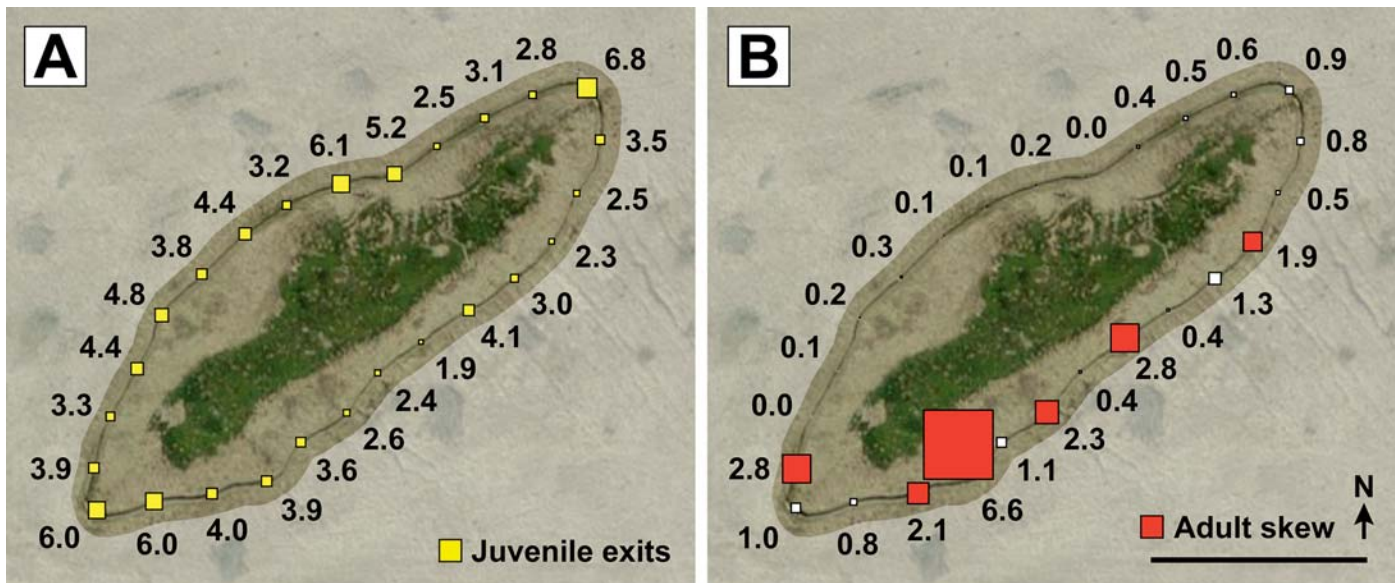


Fig. 2. (A) Newly metamorphosed juvenile Crawfish Frogs at Nate's Pond (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana) exited with no specific directionality in 2009–2011 and 2014. Exiting frogs were captured by pitfall traps (indicated by yellow squares) positioned every 10 m along the drift fence. Sizes of trap squares are proportional to the number of juveniles exiting from each trap. Numbers next to the traps show the proportion of juveniles exiting from that trap, averaged across the years. (B) Post-breeding adult Crawfish Frogs exhibited a strong tendency to exit Nate's Pond towards the southeast, presumably in the direction of their primary burrow (Heemeyer and Lannoo, 2012). A smaller subset of adults exited east; a much smaller subset exited west. Sizes of trap squares are proportional to the ratio of adults versus juveniles exiting from each trap. We included adults that originated from Nate's Pond and were captured in 2013–2016, and excluded those from 2012 (small sample size, $n = 14$). We included juveniles captured in 2009–2011 and 2014, and excluded years with small sample sizes (2013, $n = 8$) and no recruitment (2012 and 2015). Scale bar = 50 m.

Nate's Pond in all directions (Fig. 2A; $t = 1.03$, $df = 22.97$, $P = 0.314$). Nate's Pond is elliptical in shape—aligned along a southwestern to northeastern axis—and juveniles tended to exit at buckets along the long axis of the ellipse, at both southwestern and northeastern ends. Breeding took place in the central expansion.

Directions of adult migration versus juvenile dispersal.—Post-breeding adult Crawfish Frogs exhibited a southeastern directional preference (Fig. 2B; $t = -2.57$, $df = 23.76$, $P = 0.017$), which was significantly different than the random dispersal pattern displayed by juveniles exiting Nate's Pond (Fig. 2A; $t = -3.53$, $df = 18.04$, $P = 0.002$). Curiously, there was no difference between the directional preference exhibited by adult frogs that had originated from Nate's Pond and adults that had originated from other wetlands ($t = -0.01$, $df = 25$, $P = 0.991$).

Juvenile dispersal: telemetry.—Our telemetry studies confirmed our drift fence data indicating juvenile Crawfish Frogs disperse in all directions. Telemetered juveniles released at a set point adjacent to Nate's Pond dispersed without obvious directional preference (Fig. 3A, B). Similarly, juveniles released at artificial burrow entrances vectored in all directions except due east, the direction of Nate's Pond and the hill to the east of this wetland (Fig. 3C).

Telemetry data were similar but not identical between 2011 and 2015. In 2011, mean daily distance traveled was 35.1 ± 4.6 m ($\pm SE$); in 2015, mean daily distance traveled was 27.3 ± 7.5 m. In 2011, mean maximum distance traveled was 55.5 ± 10.8 m; in 2015, it was 70.4 ± 17.2 m. In 2011, mean farthest distance traveled was 63.4 ± 12.7 m; in 2015, it was 112.0 ± 35.3 m. And in 2011, mean total distance traveled was 80.4 ± 15.7 m; in 2015, it was 133.7 ± 40.1 m (Table 1). One determinant of amphibian dispersal, mean

daily precipitation, was slightly greater during the 2015 study period (2.73 ± 1.17 mm) compared to the 2011 study (2.48 ± 1.06 mm; based on hourly data recorded by the Southwest Purdue Agricultural Center–Vincennes, Knox County, IN).

Artificial burrows.—Of the 149 juvenile Crawfish Frogs released at artificial burrows, most left almost immediately, as follows (Fig. 4). During the first 24 h, 51 (34%) frogs abandoned burrows; during the next 24 h, 93 (62%) individuals abandoned burrows. Frogs released at burrows remained for an average of 2.7 days ($SE \pm 0.46$ days), although several frogs remained for much longer periods, and one frog stayed 41 days (Fig. 4). Among the frogs that remained at burrows, ten were observed to be or presumably preyed upon; these frogs disappeared following images showing snakes at or in their burrows. Confirmed predators included Common Gartersnakes (*Thamnophis sirtalis*) and an unknown bird (the telemetered carcass was located in a tree). One juvenile died of an unknown cause.

Juvenile dispersal.—Of the 196 juveniles produced at Nate's Pond subsequently captured as breeding adults, 141 (71.9%) returned to Nate's Pond to breed; the remaining 55 frogs (28.1%) dispersed to one of the other five breeding wetlands (Fig. 5A). Cattail and Big ponds received the highest numbers (20 and 19 [10.2% and 9.7%], respectively). The greatest straight-line distance traveled (to Nate's Jr.) was 1.35 km (Fig. 5A).

Breeding site philopatry.—A total of 271 adult Crawfish Frogs bred at Nate's Pond from 2012–2016 (during and after 2012, the third year of our study, we assumed unmarked animals did not originate at Nate's Pond). Of these adults, 137 (50.6%) were produced at Nate's; the remaining 134 adults

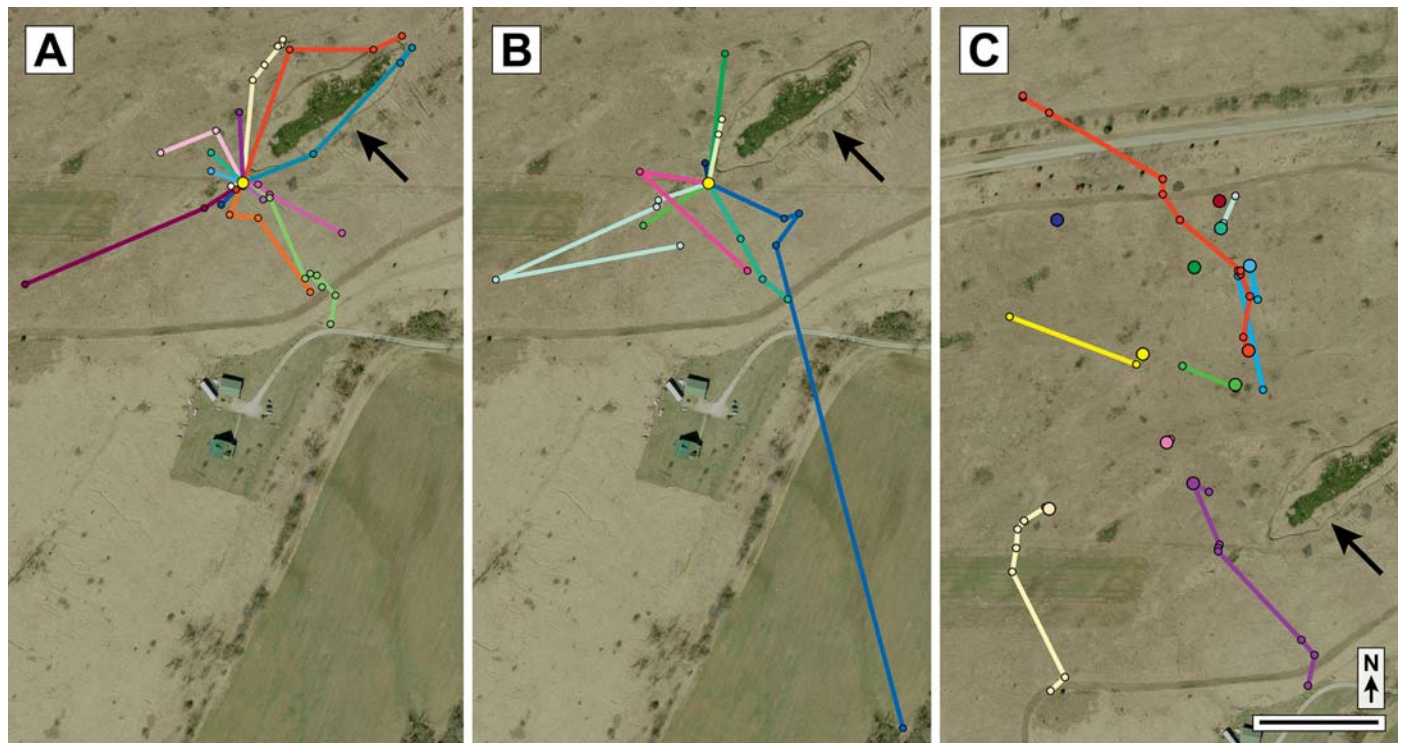


Fig. 3. Movements of telemetered juvenile Crawfish Frogs after release near their natal wetland, Nate's Pond (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana). Individuals tracked in 2011 ($n = 25$) are separated into (A) and (B) to reduce confusion from crossing telemetered paths. We released all the juveniles at the same point (the centered yellow circle) and attempted to relocate individuals every morning during the daylight. We released telemetered juveniles in 2015 ($n = 12$) at artificial burrows created between 5 and 330 meters from the drift fence (C). Each colored circle represents a relocation point for an individual. The largest circle for each colored path indicates the artificial burrow release site for that individual. Large circles without lines show frogs that did not disperse. Black arrows indicate Nate's Pond. Scale bar = 100 m.

(49.4%) had no toe clips and we assume were produced in other wetlands (Table 2). The percentage of breeding adults in Nate's Pond produced in Nate's Pond varied by year from 73.1% in 2014 to 33.7% in 2016 (Table 2).

Breeding wetland shifts.—A subset of adult Crawfish Frogs shifted breeding wetlands (Fig. 5B). Of the 255 animals captured breeding at least twice, 57 (22.4%) were found in more than one wetland. Specifically, of 15 animals that first bred at Nate's, nine subsequently bred at Big, three at Erosion Control, two at Cattail, and one at New (orange boxes, Fig. 5B). Of 14 animals that bred at Big, nine subsequently bred at Cattail, three at Nate's, one at Erosion Control, and one at New (yellow boxes, Fig. 5B). Two individuals first bred at Erosion Control and then subsequently at Big (purple box, Fig. 5B), and two bred at Nate's Jr. and then at Cattail (red box, Fig. 5B). One frog first bred at New and then subsequently at Big (green box, Fig. 5B). Finally, 23 animals that bred at Cattail subsequently bred at Big (blue box, Fig. 5B).

DISCUSSION

Between one-quarter and one-third (28.1%) of the juveniles produced at Nate's Pond subsequently recaptured as breeding adults dispersed to breed in other wetlands. The farthest dispersal distance by juveniles we measured was 1.35 km. Our data also show that adults will shift breeding wetlands; 57 (22.4%) of the 255 animals we found breeding at least twice were captured at different wetlands, including 15 adults first captured in Nate's Pond (Fig. 5B). Over the same time period, 137 of the 271 adults that bred at Nate's Pond (50.6%)

were produced at Nate's; 134 (49.4%) originated from other wetlands. This level of movement could easily explain the relatively high heterozygosity values found by Nunziata et al. (2013).

Newly metamorphosed juveniles dispersed in all directions from their breeding wetland, a result similar to the observations of Roznik and Johnson (2009a) working with Gopher Frogs. Telemetered juveniles released near the southwestern tip of Nate's Pond also dispersed in all directions (Fig. 3A, B). They generally vectored in a straight line (although see Frog 151.377, light blue line, and Frog 149.905, red line, in Fig. 3B), a second result comparable to the observations of Roznik and Johnson (2009a). Curiously, telemetered juveniles released at artificial burrow entrances tended to disperse rather than remain in the shelter of their burrows, and they too showed no directional movement preference, although none of the 12 animals moved due east. This may be an artifact of small sample size, or they may have been avoiding Nate's Pond or its adjacent hill. Aside from this, dispersing Crawfish Frog juveniles did not follow drainages, paths, treelines, fence rows, or other natural or man-made features that might reduce resistance to movement, or serve as landmarks or guides to future breeding migrations.

Comparisons with other studies.—Our conclusion that Crawfish Frog juveniles represent the dispersal stage is consistent with the literature on temperate, pond-breeding amphibians (Dole, 1971; Kupfer and Kneitz, 2000; Funk et al., 2005; Trenham and Shaffer, 2005; Gamble et al., 2007). Our results also align with previous studies showing newly metamorphosed amphibians generally disperse in all directions from

Table 1. Movement of telemetered juvenile Crawfish Frogs at Hillenbrand Fish and Wildlife Area-West (Greene County, Indiana) in 2011 ($n = 25$) and 2015 ($n = 7$). Farthest distance is the straight-line distance from the release site (not necessarily the last point), and total distance is all movement during the study period. Individuals that did not move post-release were excluded (2011, $n = 3$; 2015, $n = 5$).

Parameter	2011		2015	
	Mean $\pm$ SE	Range	Mean $\pm$ SE	Range
Days tracked	6.8 $\pm$ 0.9	1–15	4.6 $\pm$ 1.3	1–11
Body mass (g)	7.0 $\pm$ 0.1	5.2–7.4	5.3 $\pm$ 0.2	5.0–6.6
Snout–vent length (mm)	—	—	36.1 $\pm$ 1.2	34.0–44.0
Mean daily distance (m)	35.1 $\pm$ 4.6	5.1–94.8	27.3 $\pm$ 7.5	2.9–62.2
Maximum daily distance (m)	55.5 $\pm$ 10.8	5.7–296.6	70.4 $\pm$ 17.2	2.9–114.2
Farthest distance (m)	63.4 $\pm$ 12.7	2.0–343.8	112.0 $\pm$ 35.3	2.9–287.3
Total distance (m)	80.4 $\pm$ 15.7	5.8–379.4	133.7 $\pm$ 40.1	2.9–317.1

natal wetlands, while adults enter and exit breeding sites selectively, in association with suitable terrestrial habitat (Semlitsch, 1981; Madison, 1997; Sinsch, 1997; Dodd and Cade, 1998; Marty et al., 2005; Rittenhouse and Semlitsch, 2006; Semlitsch, 2008). The adults of many pond-breeding amphibian species show strong fidelity to breeding sites (Ritke et al., 1991; Madison, 1997; Kusano et al., 1999). For example, Rittenhouse and Semlitsch (2007) compiled data from 12 amphibian species and found that an estimated 95% of individuals were within 664 m of their breeding wetland edge.

We found that when Crawfish Frog juveniles dispersed to other breeding wetlands, the average distance was 826 m (SE $\pm$ 24 m), with a maximum distance of >1,350 m (Fig. 5A). These distances are greater than movements reported for juvenile Gray Treefrogs (*Hyla versicolor*; 125 m [Roble, 1979]), Coastal Tailed Frogs (*Ascaphus truei*; 360 m [Daugherty and Sheldon, 1982]), Natterjack Toads (*Epidalea calamita*; 400 m [Sinsch, 1997]), and California Tiger Salamanders (*Ambystoma californiense*; 400 m [Trenham and Shaffer, 2005]), but less than distances reported for juvenile Fowler's Toads (*Anaxyrus fowleri*; 1,650 m [Breden, 1987]), Wood Frogs (*L. sylvaticus*; 2,530 m [Berven and Grudzien, 1990]), Green Frogs (*L. clamitans*; 4,800 m [Schroeder, 1976]), Columbia Spotted Frogs (*Rana luteiventris*; 5,750 m [Funk et al., 2005]), and Northern Leopard Frogs (*L. pipiens*; 8,000 m [Seburn et al.,

1997]). However, as Dole (1971) suggests, measured dispersal distances may reflect the scale of the investigation rather than the maximum dispersal capabilities of each species. Dispersal distances also likely reflect available habitat.

We cannot calculate a precise dispersal rate, but our radiotelemetry results show juvenile Crawfish Frogs can move up to 297 m/day (Table 1). Dispersal rates vary widely for other juvenile amphibians, ranging from 800 m/day (Northern Leopard Frogs [Dole, 1971]) to 860 m in 23 days (37 m/day, Great Crested Newts [*Triturus cristatus*; Kupfer and Kneitz, 2000]) to 10 m in one year (0.03 m/day, also Great Crested Newts [Kupfer and Kneitz, 2000]). Dispersal rates will vary with environmental conditions, and in Crawfish Frogs are best correlated with rain (Swan, 2016).

Dispersal.—As noted above, when offered artificially constructed crayfish burrows as retreat sites, Crawfish Frog juveniles almost immediately abandoned them (average duration of residency = 2.7 days) in order to continue dispersing (Fig. 4). While it may be that Crawfish Frogs were simply abandoning artificial burrows because they found them unnatural, four crayfish (*Cambarus polychromatus*) adopted these burrows—two occupied a burrow for a single night; two others capped their respective burrows and established residency. We assume from these observations that our artificial burrows were suitable retreat sites (i.e., if crayfish will inhabit artificial burrows as if they were

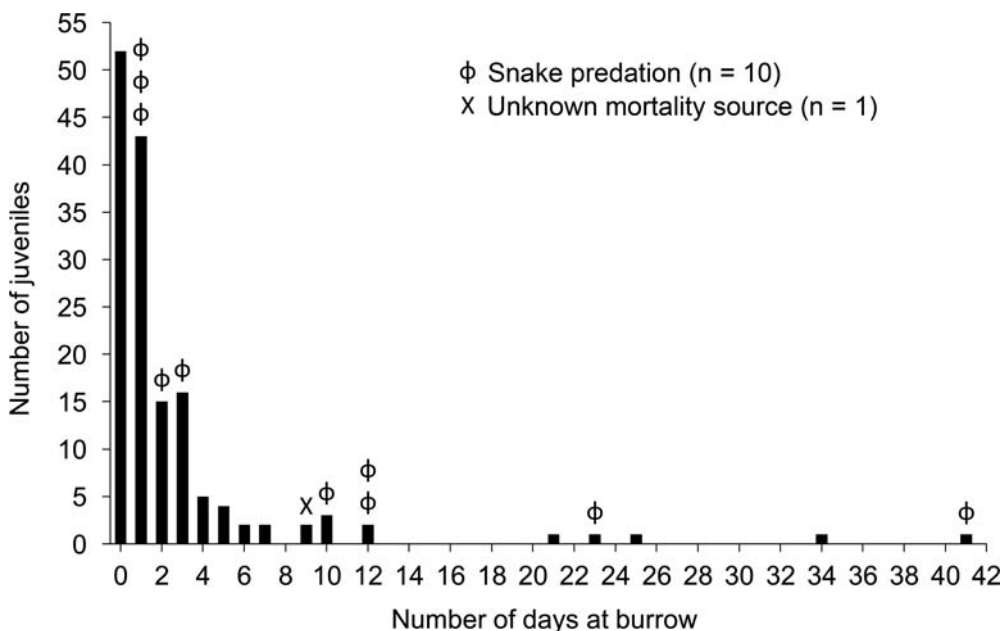


Fig. 4. Retention of juvenile Crawfish Frogs released at artificial burrows west of Nate's Pond (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana). From 24 June–1 August 2015, we used wildlife cameras to determine burrow occupancy. We defined snake predation as instances when frogs no longer appeared after a snake was photographed at burrows. Snake predation ($n = 10$) and an unknown case of mortality ($n = 1$) are noted.

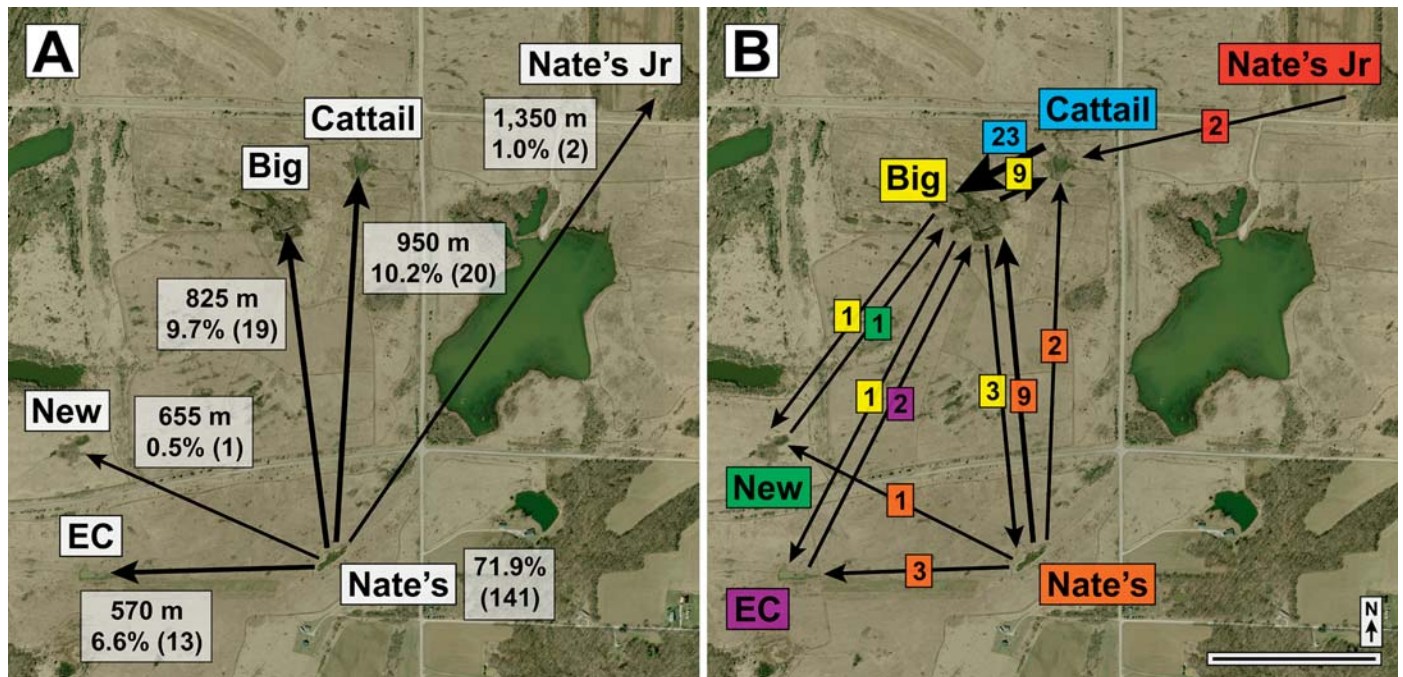


Fig. 5. (A) Crawfish Frog movement from Nate's Pond (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana). One-third of juvenile Crawfish Frogs that metamorphosed at Nate's Pond dispersed to nearby wetlands to breed. Two-thirds of juveniles returned to Nate's to breed. Numbers in parentheses represent counts of individuals. The sizes of the arrows are proportional to the number of individuals. (B) A subset of adult Crawfish Frogs shifted breeding wetlands between years. Colors match the initial wetland from which frogs emigrated. Numbers indicate counts of individuals moving between wetlands. Scale bar = 500 m.

authentic, one supposes Crawfish Frogs would also find them suitable if they were predisposed to stop dispersing and occupy a burrow.) In fact, a handful of Crawfish Frog juveniles released in burrow entrances remained for weeks at these burrows (Fig. 4).

As a result of this dispersal, we found juveniles from Nate's Pond in every Crawfish Frog breeding wetland at our study

site (Fig. 5A). There was no clear dispersal pattern. For example, the pond with the largest breeding population (Big Pond) received only the second-highest number of animals, while the most distant pond (Nate's Jr.) received only the second-lowest number. It is unlikely that the probability of snake and bird predation is equal across all portions of this landscape; disproportionate predation on juvenile Crawfish

Table 2. Captures of first time breeding and recaptured adult Crawfish Frogs at Nate's Pond (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana) from 2012 through the 2016 breeding seasons. We identified individuals originating from Nate's Pond using cohort toe clips given to newly metamorphosed frogs from 2009–2015, and assume that frogs without clips originated from other local wetlands. We excluded captures prior to 2012 since unmarked animals may have metamorphosed from Nate's before our study began in 2009. Percentages are captures from each cohort (Nate's or other wetlands) divided by all frogs captured that year (all captures).

Origin wetland	2012	2013	2014	2015	2016	Total
Nate's Pond						
Total (% of all captures)	13 (65.0%)	79 (70.5%)	68 (73.1%)	26 (45.6%)	31 (33.7%)	217 (58.0%)
First capture	13	71	30	7	16	137
Recapture	—	8	38	19	15	80
Male	13	46	40	15	18	132
Female	0	33	28	11	13	85
Other wetlands						
Total (% of all captures)	7 (35.0%)	33 (29.5%)	25 (26.9%)	31 (54.4%)	61 (66.3%)	157 (42.0%)
First capture	7	31	19	25	52	134
Recapture	—	2	6	6	9	23
Male	4	19	17	22	32	94
Female	3	14	8	9	29	63
All captures						
Total	20	112	93	57	92	374
First capture	20	102	49	32	68	271
Recapture	—	10	44	35	24	103
Male	17	65	57	37	50	226
Female	3	47	36	20	42	148

Frogs (the overall likelihood of survival to first breeding is 3.5–4.0%; Kinney, 2011; Stiles and Lannoo, unpubl. data) could explain these differences.

The direction and strength of juvenile dispersal differed from the direction and strength of adult migration (Fig. 2A, B), which Roznik and Johnson (2009a) also found to be true for Gopher Frogs. Presumably these observations reflect the difference between dispersal movements (scattered, to places never experienced by newly metamorphosed animals) and migration movements (directed, by adults vectoring back to their primary burrow; Heemeyer and Lannoo, 2012). In a relatively uniform upland habitat, migration directions would mirror dispersal directions. But few habitats, including unbroken tallgrass prairie, are uniform, and the differences between migration and dispersal directions likely reflect relative amounts of quality upland habitat (in the case of Crawfish Frogs, high crayfish burrow densities). As noted above, these differences in directional preference could possibly reflect other strong ecological relationships, such as variation in predator densities.

Dispersal as a predator avoidance mechanism?—Roznik and Johnson (2009b) found that burrow habitation was critical to the survival of juvenile Gopher Frogs. Specifically, their data show that Gopher Frog juveniles in burrows were 25 times less likely to be preyed upon than juveniles without such cover. In fact, the only frogs that survived until the end of their study were animals that found burrows within eight days and remained there for the next six weeks. Exposed frogs tended to be preyed upon by mammals and birds, and especially snakes. From this result we can conclude that seeking shelter has a selective advantage to an individual when compared with dispersing. On the flipside, classic metapopulation theory holds that movements among populations are advantageous by repopulating habitats, avoiding inbreeding, and maintaining densities (e.g., avoiding the Allee effect; Hanski, 1998). The decision by an individual frog whether or not to disperse would seem to be a classic case of pitting self interests against group interests.

We made three observations that suggest this dichotomy is false for juvenile Crawfish Frogs. The first, based on wildlife camera images of juvenile Crawfish Frogs at burrows, is that juvenile Crawfish Frogs choose burrows with a diameter similar to those used by adults, even though large numbers of smaller burrows are available at HFWA-W (Heemeyer et al., 2012; Swan, 2016). The second, following from the first, is that juvenile Crawfish Frogs achieve little reprieve from predators by occupying these large crayfish burrows (Swan, 2016). While Crawfish Frog adults use burrows to protect them from predators as well as buffer environmental extremes (Engbrecht et al., 2012; Heemeyer and Lannoo, 2012; Heemeyer et al., 2012), juveniles apparently use them only to buffer environmental extremes. Adult Crawfish Frogs never venture farther than two or three frogs lengths from their burrow entrance and will form a “feeding platform” as they wear away the vegetation where they position themselves. When frightened, adults make one hop into their burrow, turn around to face the entrance, inflate their bodies, and lower their heads, and are thus afforded protection (Altig, 1972; Engbrecht et al., 2012). Juvenile Crawfish Frogs, on the other hand, range widely from their burrow entrance, putting themselves in a position to have little chance to reach their burrow entrance during predator attacks. Further, because juveniles naturally tend to occupy adult-sized burrows (Stiles et al., unpubl.), they cannot inflate their

bodies against the burrow wall and lower their head to dissuade predators, as adults will (Altig, 1972; Engbrecht et al., 2012).

Our third observation is that once Crawfish Frog juveniles locate a burrow, their overwhelming response is to abandon it in order to continue dispersing (Fig. 4). Unlike in Gopher Frogs, juvenile Crawfish Frogs apparently have a strong drive to disperse, and not only would time spent in retreat sites slow down their rate of dispersal, given the size of the burrows they choose and their behavior at them, burrow habitation might not reduce the rate of predation. We suspect that aside from avoiding hot, dry conditions, burrows might not confer any survival advantage to newly metamorphosed juvenile Crawfish Frogs, suggesting that Roznik and Johnson's (2009a, 2009b) conclusion about the value of retreat sites in avoiding predators in Gopher Frog juveniles does not extrapolate to Crawfish Frogs.

Instead, we offer the contrary proposition that dispersal itself offers the opportunity to avoid predation in juvenile Crawfish Frogs. Arnold and Wassersug (1978) suggested that synchronous metamorphosis in pond-breeding amphibians serves to satiate predators—that juvenile amphibian numbers simply overwhelm the capacity for predators to respond and that some juveniles therefore must survive. They also note the tendency of certain snake species, such as Gartersnakes (*Thamnophis* sp.), to be attracted to the margins of ponds during amphibian metamorphosis. Given this, our first point is Crawfish Frog juveniles would confer a substantial survival advantage by getting as far away from a wetland edge as quickly as possible.

Our second point is because juvenile Crawfish Frogs do not defend themselves against predators using burrows, as adults will, predation becomes a function of frog/predator encounter rate. Assuming that beyond the wetland margin, predator density is uniform across a generally featureless grassland, Crawfish Frogs will decrease their encounter rate with predators by decreasing their density across the landscape and can only decrease their density by dispersing (of course, predation will also accomplish this). The post-metamorphic tendency by juvenile Crawfish Frogs to disperse appears to continue for some period of time (it must for frogs to be found 1.35 km from their breeding wetland given an average movement of ~ 30 m/d), which creates an enormous density advantage for Crawfish Frog juveniles. Using the equation for the area of a circle ($=\pi r^2$), let us say 1,000 metamorphosing frogs are concentrated in the center of a drying wetland. Assuming no mortality, after the first dispersal movement, a distance of 55 m in 2015 (70 m in 2011; Table 1), juvenile Crawfish Frogs increase their area occupied to 9,503 m², or one frog every 9.5 m² (most frogs will not move the maximum distance so will be distributed within this area). After the second movement, again 55 m, their density becomes one frog every 38 m². After the third movement, their density becomes one frog every 86 m², and so on in a geometric progression. After a few weeks of such movements, at a distance of 500 m, the mean burrow distance of adults from breeding wetlands observed by Heemeyer et al. (2012) and Heemeyer and Lannoo (2012), the density becomes one frog every 78,000 m². For Crawfish Frogs, dispersal does not only serve to increase connectivity among populations, it may also serve as an antipredator behavior.

Management implications.—Except when breeding, Crawfish Frogs are terrestrial. Early descriptions comparing them to bufonid toads (both have dry, warty skin and use body

inflation as a predator deterrent) are not phenotypically inaccurate. Heemeyer et al. (2012) noted the extreme dependence of Crawfish Frogs on crayfish burrows. (They generally occupy a single primary burrow throughout the non-breeding season and will return to this same burrow following breeding events. Since Heemeyer's study, we have observed three frogs occupying their respective burrows for five consecutive years.) Based on the importance of burrow integrity, Heemeyer et al. (2012) recommended a 1 km, no-plow buffer, including eliminating strip-disking, around breeding wetlands in order to protect Crawfish Frogs from being killed or maimed by the plow share or mouldboard, and to protect habitat quality by maintaining intact crayfish burrows. Given the data we present here, it would also be wise to manage against death in juvenile Crawfish Frogs (Rothermel, 2004). Ways to accomplish this include minimizing summertime aboveground disturbance through the use of mowers, all-terrain vehicles, trucks, and heavy equipment. Plowed areas such as food plots should be narrow and placed in a radial pattern in relation to breeding wetlands to preclude juveniles crossing tangentially oriented areas of bare ground, which expose them to predators.

Roznik and Johnson (2009a, 2009b) found that areas of longleaf pine savanna maintained by prescribed burning had a higher density of burrows that Gopher Frogs could use as retreat sites. The story is likely similar for Crawfish Frogs. Our entire study site is being maintained as grassland using prescribed burning and occasional timbering. Within this relatively uniform habitat, the sites most used by Crawfish Frogs are well-drained crayfish burrows. Unlike Roznik and Johnson (2009a, 2009b), we could not make comparisons between habitat suitability in managed and unmanaged areas, but without upland crayfish burrows, fishless breeding wetlands, and the ability of both juvenile and adults to move among these habitats, Crawfish Frog populations will be extirpated.

ACKNOWLEDGMENTS

We thank S. Klueh-Mundy, B. Feaster, T. Stoelting, K. Smith, and R. Ronk for their support and for access to Hillenbrand Fish and Wildlife Area. We thank N. Engbrecht and J. (Heemeyer) Beck for project initiation and data collection, and H. Nesius, L. Sawyer, A. Hoffman, A. Whitlock, L. Neumann, and M. Goode for field research assistance. Lastly, we thank J. Klemish and S. Lannoo for both field assistance and commenting on earlier drafts. This project was supported by a State Wildlife Grant (number E2-08-WDS13) awarded by the Indiana Department of Natural Resources, a research grant awarded by Prairie Biotic Research, Inc., and a student stipend scholarship awarded by Peabody Energy. All procedures were in accordance with the Institutional Animal Care and Use Committee (IACUC) numbers 245168-1:ML, 628051-1:ML, and 705946-1:ML issued by Indiana State University and Scientific Purposes License numbers 09-0084, 10-0027, 11-0017, 12-0015, 13-072, 14-063, 15-013, and 16-058 issued by the Indiana Department of Natural Resources.

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